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# Abert Squirrels Influence Nutrient Transfer through Litterfall in a Ponderosa Pine Forest<sup>1</sup>

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## Abstract

Study objective was to determine the influence of Abert squirrels on transfer of nutrients, specifically nitrogen and carbon, from trees to the forest floor. Increase in total N and C in litterfall because of squirrel activities was associated primarily with the increase in total mass of litterfall. Abert squirrels made their most significant contribution to the nutrient transfer process through clipped twigs which had an N concentration nearly double that of "natural" litterfall.

**Keywords:** *Sciurus aberti*, litterfall, nutrient transfer.

In this paper we report results of a combined study of Abert squirrels (*Sciurus aberti*) and the nutrient regime. Nutrients are frequently a limiting factor in forest ecosystems, and are usually influential in ecosystem productivity. Animal life has been studied extensively in terms of its contribution to decomposition processes in the nutrient cycle, but has been virtually forgotten with respect to the restitution phase, especially litterfall. Animals may play an important role in this part of the nutrient cycle. The objective of this study was to determine the influence

of the Abert squirrel on transfer of nutrients, specifically nitrogen (N) and carbon (C), from trees to the forest floor.

## Methods

Field studies were conducted in the vicinity of Fort Valley Experimental Forest, near Flagstaff, Ariz. The study site was characterized by an open stand of large pole and small saw timber ponderosa pine with little understory vegetation on rolling slopes (fig. 1). Soils were derived from basalt and appeared to be of the Brolliar Series. An area of about 9.2 hectares was searched to locate and tag all squirrel nest and "feed" trees. Feed trees were defined as trees in which squirrels exhibited medium to heavy feeding activity. A total of 43 feed trees and 27 nest trees were found. Fourteen of each were selected at random for study. In addition, 14 control trees were randomly selected from a pool of 30 trees; these trees were similar to the nest and feed trees but showed no evidence of squirrel use.

A two-stage sampling system was used. Litter traps (50 cm x 50 cm) made of 1/8-inch hardware cloth (Davis et al. 1968) were located at random in the "tree influence zone" of each of the 42 trees for periodic collections. The tree influence zone was the

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Figure 1.—The study site was characterized by an open stand of large pole and small saw timber pine with little understory vegetation.

area directly under the canopy but extending one meter beyond its projected perimeter. These influence zones were delineated on the ground, and a sufficient number of traps placed under trees to cover 10% of the zone (average number of traps was 10 per tree).

In addition to litter sampled with traps, all litter known to have fallen to the forest floor because of squirrel activity was collected by hand from outside the litter traps but within the tree influence zone. This sample was collected to permit a more adequate estimate of major litter transfer by squirrels. The traps provided a check on the "hand" sampling, an estimate of the difference between control, nest, and feed trees, and a measure of small litter transfer by the squirrel (material that could not be detected without the aid of a trap).

Litter was collected between the 22nd and 25th of August, September, November, January, April, May, and July of 1974-75. Because of the variable interval between sampling dates, litterfall data were expressed on a monthly basis for comparison and statistical analyses.

Trap collections under a single tree were pooled by date and separated according to needles, bark and twigs ( $\leq 1$  cm in diameter), cones (including bracts and seeds), and "other" components (including twigs clipped by squirrels, peeled twigs, mistletoe, nest parts, and fallen twig ends). Needled twig ends lost from the forest canopy because of natural causes such as wind or storms were defined as fallen twig ends and were distinguished from squirrel clippings by the absence of easily identifiable teeth marks from

the squirrel's bite (Rasmussen et al. 1975). Nests were taken apart and separated into twigs, needles, grass, and other material. Samples were oven dried at 70°C, weighed, and ground to pass a 40-mesh screen. The material was then analyzed for total nitrogen by the salicylic acid modification of the Kjeldahl procedure (Bremner 1965) and organic carbon by dry combustion using a high-frequency induction furnace (Allison et al. 1965).

T-tests were used to test hypotheses of no differences between treatment means.

## Results

At the end of the field study, sample trees were reexamined as to the accuracy of the presampling tree classification. Of the 14 trees classified as feed trees at the outset of the study, only 6 were used as feed trees during the study.<sup>3</sup> Of the 14 nest trees, which also served to some extent as feed trees in 1973-74, only 8 were fed upon (6 heavily) in 1974-75. The control trees, with one exception, again were not used by squirrels during the field study.

To accomplish the objectives of the study, it was necessary to reclassify the sample trees in accordance with the actual use by squirrels during the sampling period. Because litterfall of nest and feed trees was similar, and because many nest trees served also as feed trees, the nest tree classification was dropped and sites were reexamined on the basis of feeding activity alone. Comparison revealed no differences in physical characteristics between the 13 established feed trees and the 13 remaining control trees.

## Composition and Amount of Litterfall

The effects of Abert squirrels on the amount and distribution of litterfall from feed trees are summarized in table 1. Total litterfall from feed trees was 90 g/m<sup>2</sup>/yr greater (50% more) than that from control trees, and the increase by components ranged from 25% for needles to 28 times for "other" litterfall; the latter category was increased from 1 g/m<sup>2</sup>/yr for control trees to 32 g/m<sup>2</sup>/yr for feed trees. On a yearly basis only cone-fall was unaffected by squirrels.

Needle-fall averaged 181 g/m<sup>2</sup>/yr for control and feed trees, or about 76% of total litterfall. The latter figure is comparable to other forests (Bray and Gorham 1964, Rodin and Bazilevich 1967). Needles made up more than 90% of litterfall from September through November, the peak period for litterfall for pine forests (Bray and Gorham 1964, Stark 1973). In only one period, June-July, did another litterfall component (bark and twigs) outweigh needles. Needles were mostly old and dry, except during early

<sup>3</sup> According to D. R. Patton (personal communication), there is now some evidence that Abert squirrels rotate their use of trees for feeding from year to year.

Table 1.—Average amount of dry matter in litterfall for the year and distribution among components for control and feed trees

Component of litterfall	Control trees		Feed trees		Pooled st'd error	Significance of t-test <sup>1</sup>
	g/m <sup>2</sup> /yr	%	g/m <sup>2</sup> /yr	%		
Needles	161.1	81.8	200.9	70.0	16.7	.05
Bark and twigs	28.5	14.5	41.8	14.6	5.6	.05
Cones	6.4	3.2	12.1	4.2	5.1	n.s.
Other	1.1	.05	32.1	11.2	10.3	.01
Total litterfall	197.1	100.0	286.9	100.0	24.4	.01

<sup>1</sup>0.05 level of probability.

spring when many green needles were found in litterfall. Periodic snow storms and increased squirrel activity are probably associated with fall of green needles in spring.

Litterfall from feed trees contained 13 g/m<sup>2</sup>/yr more bark and twigs than from control trees (table 1), but the proportion of bark and twigs in litterfall was unchanged at 14.5%. Except for the later winter period for feed trees and the June-July period, bark and twigs were the second most abundant litterfall category. In most cases, bark and twig litterfall appeared old and dry.

Cone litterfall consisted of mature cones that fell from trees after seed dispersal, a few immature ovulate cones still tightly closed, the small but numerous staminate cones in early summer, and various cone parts (seeds, seed wings, and scales). Cones accounted for only 3.8% of all litterfall trapped, and this consisted primarily of old cone bracts.

Chewed cones (cones from which bracts and seeds had been removed) also were found in litterfall, particularly during late summer and fall (July-November). During the study, chewed cone material accounted for only a small part of squirrel-activated litterfall, but this percentage could increase (or decrease) with the variable production of cones. In 1974-75, only one of the 26 trees—a feed tree—was used heavily by squirrels for cone feeding.

Mistletoe was a minor but consistent component of "other" litterfall. Other litterfall common to both feed and control sites was "fallen twig ends".

Clipped twigs, by definition, were found only under feed trees (fig. 2). The number of clipped twigs collected per tree annually ranged from 6 to 118; the total number of twigs clipped during the year for all 31 feed trees was 392. The average weight of a clipped twig was approximately 10 grams, about 80% needles and 20% wood and bark. Clipped twigs were young and frequently had drops of recent sap flow at the clipped end. Attached needles were green and fresh. Clipped twigs were frequently accompanied by peeled twigs (fig. 3) whose inner and outer bark had been removed. On occasion, chewed outer bark, which gave every appearance of having been peeled from a twig, also was found in litterfall.

If the weight of needles from clipped twigs (22 g/m<sup>2</sup>) and the weight of wood and bark from clipped twigs and peeled twigs (6.9 g/m<sup>2</sup>) are added to the weight of needles and bark and twigs for feed trees shown in table 1, the overall influence of squirrel activity on these two dominant categories of litterfall can be calculated. This total added figure for needlefall is 222.9 g/m<sup>2</sup>/yr, or a 39% increase over that of the control trees; the total for bark and twigs is 48.7 g/m<sup>2</sup>/yr or a 71% increase over the control.



Figure 2.—Ponderosa pine twigs clipped by Abert squirrels.



Figure 3.—Ponderosa pine twigs peeled by Abert squirrels.

Nest parts were a third component of litterfall occasionally found under feed-nest trees. This duff-like material was a loose mixture of bits of grass, shredded bark, and needles all packed together. Where nest duff was a part of litterfall, the nests appeared to be in good shape and not in a state of decay. However, it was very difficult to determine by appearance alone whether or not a nest was being used currently by squirrels. Presence of squirrel clippings under a nest tree may be solely the result of feeding activity.

During late winter (February-April) significantly greater amounts of needle, bark, and twig litterfall were found under feed than control trees (fig. 4). The sum of cone, needle, bark, and twig components as well as total litterfall (including "other"), was also greater under feed trees. The only other significant difference was in June and July when needlefall from feed trees was greater than from control trees.

During the February-April period, when differences between feed and control trees were noted in most litterfall components, the weight of "other" litterfall also reached a peak (fig. 4). Other components comprised more than 40% of litterfall of feed trees during this period, but accounted for only 2.3% of the litterfall of control trees. Although squirrels clipped twigs throughout the year (table 2), the greatest amount of clipping took place during the winter, a phenomenon reported by other observers (Pearson 1950, Keith 1956, Stephenson 1975). Of all "other" components, clipped and peeled twigs accounted for 94% of the weight (89% clipped twigs, 5% peeled

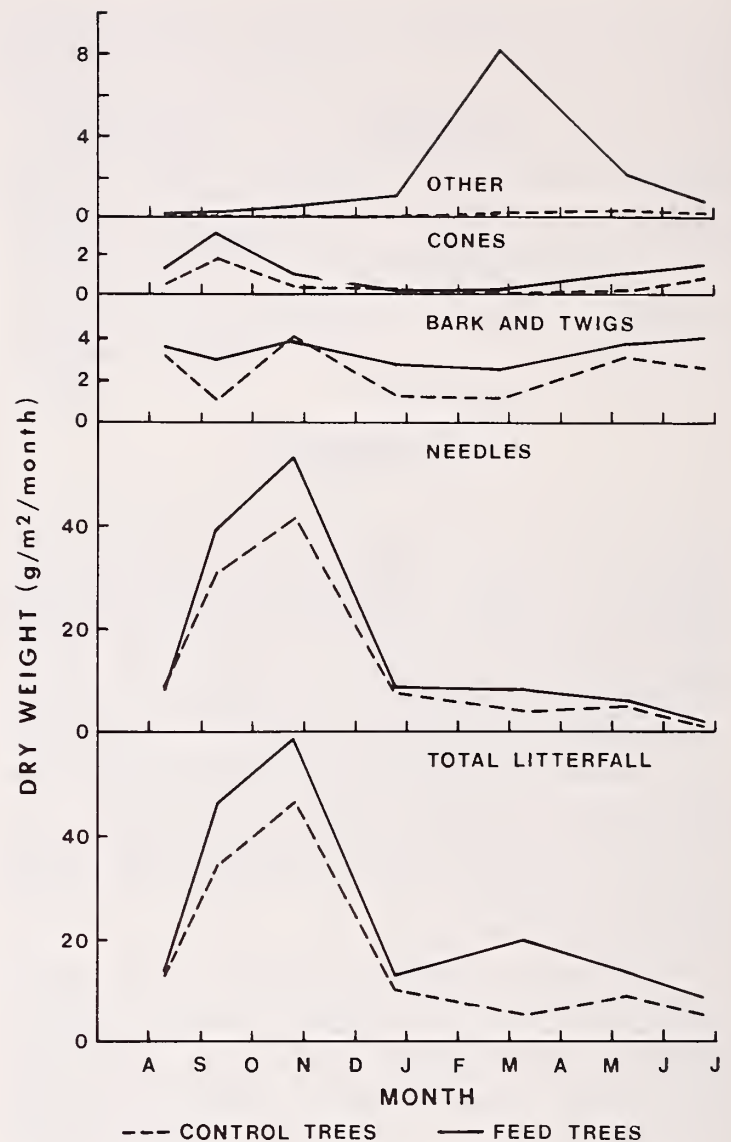


Figure 4.—Dry weight per month of litterfall from feed and control trees for seven collection periods.

twigs); mistletoe, fallen twig ends, and nest duff accounted for the rest. Under control trees, "other" litterfall contained only mistletoe and fallen twigs, the latter accounting for the major part (64.6%).

Table 2.—Number of clipped twigs (trapped and untrapped) found in the tree influence zone of feed trees for each collection period

Collection period	Months	Number of clipped twigs
July-Aug.	1	1
Aug.-Sept.	1	20
Sept.-Nov.	2	29
Nov.-Jan.	2	36
Jan.-Apr.	3	257
Apr.-May	1	22
May-July	2	27

## Nutrient Content

### Concentration of Nitrogen and Carbon

With the exception of cone material, no significant differences in percentage N of litterfall components common to both feed and control trees were found for any of the collection periods (fig. 5). Percentage N of

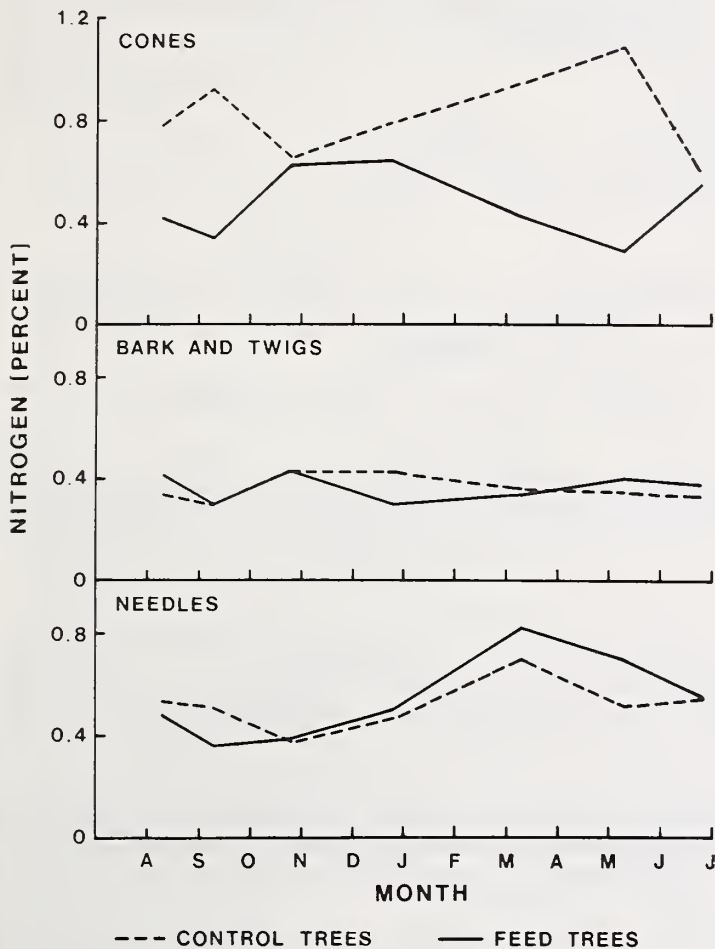


Figure 5.—Percentage nitrogen of needle, bark and twig, and cone components of litterfall for feed and control trees for seven collection periods.

cone litterfall under control trees was higher than that of feed trees in May. As percentage N of cone material from feed trees declined from October to May, percentage N of cone material of control trees increased (fig. 5). Cone litterfall of feed trees was found to contain fewer seeds and more bracts than that of control trees. Because seeds had higher N content than chewed cones or bracts, the presence of more seeds in cone material under control trees may help explain the higher N concentration of cone litterfall from control trees.

The seasonal trend in N concentration of needle litterfall was similar for both treatments (fig. 5). Nitrogen concentration was highest during late

winter and early spring (February-April) and lowest in fall and early winter. Nitrogen concentration in needles from clipped twigs was consistently higher than that of natural needlefall for all collection periods. Over the year, needles of clipped twigs averaged 1.13% N versus only 0.57% N in naturally cast needles. The N percentage of twigs and bark from clipped twigs also was greater than that of "natural" litterfall (0.60% versus 0.37%).

Nitrogen is a mobile element associated with areas of new tissue growth (Kramer and Kozlowski 1960). A gradation in N concentration was noted within clipped twigs from the clipped end to the terminal bud.<sup>4</sup> Percentage N was 1.4% in the terminal bud, 1.1% within the next half-inch and only 0.4% in the half-inch just above the point of clipping. Although the parts of the tree selected by squirrels for their food are among the highest in N concentration, we have no basis for saying that squirrels select food on the basis of N content.

The component of natural litterfall most comparable to clipped twigs is fallen twig ends. These needled twigs were found under both feed and control trees. Needles of fallen twig ends were generally higher in N concentration than naturally cast needles. However, the N percentage of needles from fallen twig ends was only half that of needles from clipped twigs. The lower concentration of N in needles of fallen twig ends is probably associated with a developing state of senescence. As needles begin senescence, they apparently lose the ability to retain the more mobile elements (such as N) in competition with more physiologically active regions (Kramer and Kozlowski 1960). Parts of vegetation that are caused to fall "prematurely" probably contain more N than "naturally falling" material (Gosz et al. 1972). Little difference was noted between the percentage N of twigs and bark of fallen twig ends and that of clipped twigs.

Mistletoe contained 1.1% N. The N concentration of nest duff was also high (1.54%). The mean N concentration of peeled twigs was 0.33%, a value less than that of twigs and bark of natural litterfall. Analysis of a half-peeled twig dropped by a squirrel interrupted while feeding showed the unpeeled half contained 0.38% N, the peeled half 0.31% N. Chewed bits of bark stripped from a twig contained 0.46% N. Thus, the outer and inner bark of small twigs appear to have a greater N concentration than the inner woody portion. We did not analyze inner bark separately, but Patton (1974) found an inner bark sample of ponderosa pine that contained 0.67% N.

Components of litterfall did not differ in C concentration between feed and control trees. Nor did season of the year have any influence on C content of

<sup>4</sup>Samples of clipped twigs taken for chemical analysis were generally removed from the portion of the clipped twig most distant from the terminal bud. The N concentration of the twig portion of clipped twigs presented is thus somewhat conservative.

litterfall. The variations observed in figure 6 were apparently the result of experimental error and random variation. Carbon content of all three litterfall components (needles, bark and twigs, cones) varied less than 4% during the entire year (fig. 6).

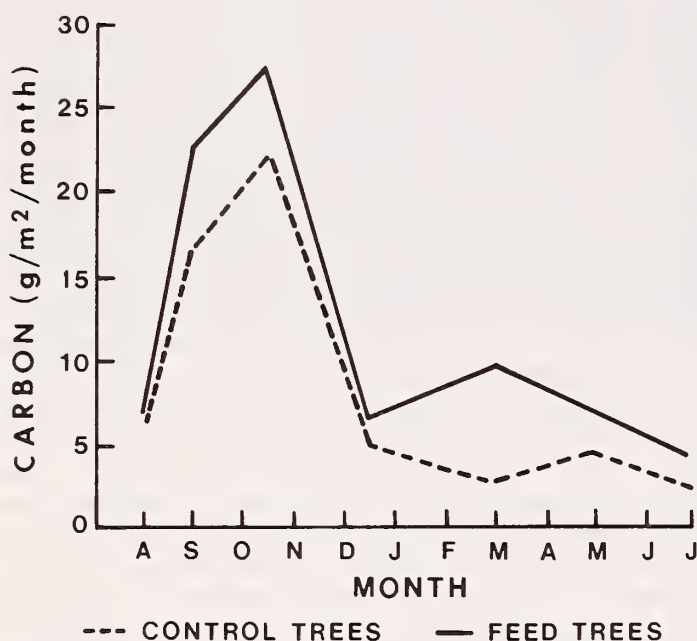


Figure 6.—Percentage carbon of needle, bark and twig, and cone components of litterfall for feed and control trees for seven collection periods.

No difference in C concentration was found between needle, bark and twig material of clipped twigs and that of fallen twig ends. Nor did percentage C differ between clipped twigs and components of “naturally” fallen litterfall. The chewed bits of bark apparently discarded by squirrels in the process of stripping twigs contained 51% C. The C content of peeled and unpeeled halves of the twig mentioned earlier were 49.2% and 50.3% respectively. The mean C concentration of mistletoe was 49.0% and that of nest duff only 43.3%.

#### Amount of Nitrogen and Carbon

Graphs (fig. 7) portraying amount of N transferred in litterfall from control and feed trees as a function of time are similar in appearance to those for dry weight (fig. 4). Late winter-early spring was the only period when total litterfall of control and feed trees differed significantly in weight of N, but the difference was large. During the February-April period, N in bark and twig, needle, and “other” litterfall components was greater under feed trees. Nitrogen transfer by needlefall also was greater from April to May and from June to July. The large difference between treatments in N for the “other” litterfall category was primarily the effect of clipped twigs under feed trees and led to the difference between treatments in N of total litterfall.

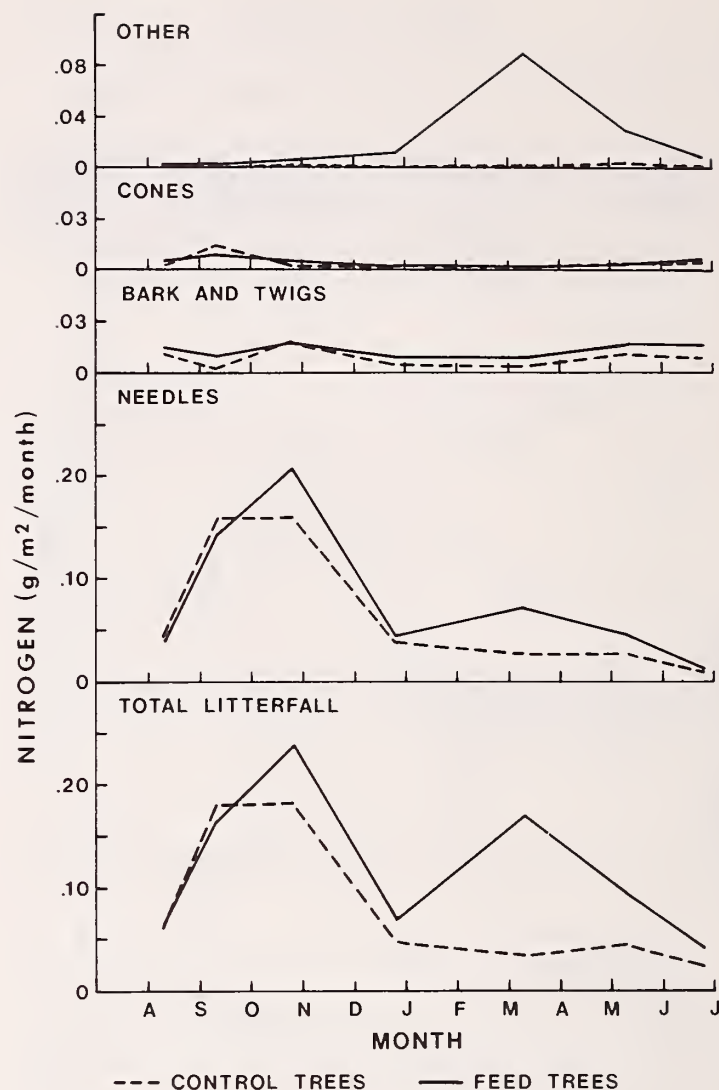


Figure 7.—Weight of nitrogen transferred per month from standing crop to the forest floor by litterfall of feed and control trees for seven collection periods.

In trees where squirrels actively fed, 15.3 kg/ha/yr of N were transferred to the forest floor (fig. 7), a significantly higher amount (70% higher) than from control trees. In the control treatment, only 9.0 kg/ha/yr of N were transferred via litterfall to the forest floor. Most of this N (81.6%) was transferred in the needlefall. Cone material, which accounted for only 3.2% of the total weight of litterfall, contributed almost 5.5% of the N in litterfall. Bark and twigs were low in N concentration but accounted for 11.9% of N in litterfall while “other” litterfall comprised 1.1% of the N.

The mean amount of N that fell in litterfall over the entire year was 12.2 kg/ha, considering both feed and control trees. This compares with 12.4 kg/ha/yr of N in an eastern deciduous forest (Wells et al. 1971). On a world basis, Rodin and Bazilevich (1967) reported the return of N to the forest floor in the coniferous zone varies between 10 and 50 kg/ha/yr and ranges even higher in plantations.

Because percentage C in litterfall varied little among components or between treatments, any difference between treatments in amount of C

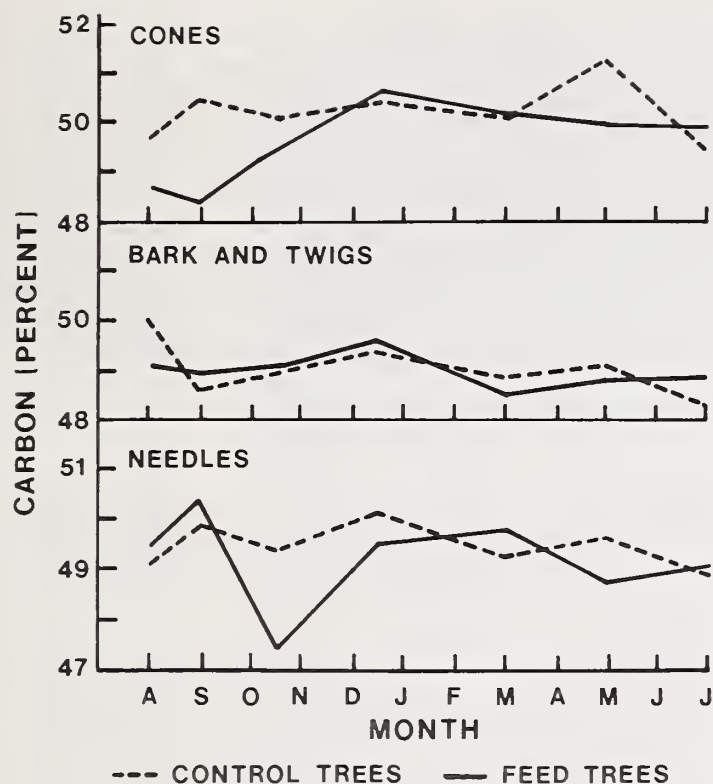


Figure 8.—Weight of carbon transferred per month from standing crop to the forest floor by total litterfall of feed and control trees for seven collection periods.

transferred via litterfall (fig. 8) is similar to differences noted in litterfall weight between treatments (fig. 4). When the total amount of C that fell via all litterfall components over the entire year is tallied, a significantly greater amount, almost 50% more, was found under feed than control trees. As was true of N, differences between treatments were observed only in late winter. From February to April, 3.6 times as much C was transferred through litterfall of feed trees as control trees. Amount of C in litterfall of feed trees exceeded that for control trees for all components except cone material.

### Nest Characteristics

Although the nest of the Abert squirrel is roughly spherical, a small platform often extends beyond the bowl edge on one side. Nests are usually constructed on a large limb and against the bole of the tree, though on occasion nests were noted in the fork of large branches or out on a limb.

Twigs and branches made up 42% by weight of the structural components of the nest. Needles were the next largest component (26%) followed by loose (20%) and packed duff (12%). Packed duff, composed of an almost indistinguishable mass of pine needles, excrement, and other organic matter, had the highest N concentration (1.94%) of the four nest components. Loose duff had an N content of 1.54%, needles 1.26%, and twigs and bark only 0.6%. Loose and packed duff contained almost half the nest N.

Needles, twigs and bark of nests had a higher percentage N than did similar components of litterfall, probably because of excrement in the nest. Fecal pellets contained 2.3% N. Percentage C of needles, twigs and bark from nests was similar to that of litterfall. Percentage C of loose and packed duff (43.4% and 39.8%) was lower than any component of the litterfall.

Although N percentage of bits of nest duff found in litterfall was comparatively high, an average of only 0.37% g/m<sup>2</sup>/yr of nest duff was found in litterfall of nest trees. If the rate of transfer of other nest components is comparable to that of duff material, it would be years before nutrients in the average nest were returned to the forest floor, except for soluble nutrients. These nutrients are probably returned on a continuing basis by throughfall and stemflow.

### Conclusions

Abert squirrels had a significant effect on transfer of nutrients by litterfall from the standing crop to the forest floor for ponderosa pine trees inhabited and used for feeding by the squirrels. The squirrels' influence was expressed not only in clipped and peeled twigs discarded during the feeding process, but also in the fall of senescing needles and bits of bark and twigs. Undoubtedly, much of the loose needle, bark, and twig material found in litterfall is discarded from twigs in the process of feeding on inner bark, but it is possible squirrels also break off tree parts while climbing about looking for twigs. Trees with squirrel nests also had occasional minor amounts of nest parts in their litterfall. No difference was noted in nutrient transfer via litterfall between trees that served both as nest and feed trees and those that were used only as feed trees.

Although squirrels clipped twigs throughout the year, by far the greatest amount of clipping took place during late winter and early spring. This peak in feeding activity helps explain the differences found between treatments in litterfall from February to April and the trend in total litterfall differences between treatments in May to June.

Increase in total N and C in litterfall because of squirrel activities was associated primarily, though not solely, with the increase in total mass of litterfall, because percentage C varied very little among components. However, litterfall components did differ in percentage N. The N concentration of clipped twigs was nearly double that of comparable components of "natural" litterfall. It was through the clipped twig component of litterfall that Abert squirrels made their most significant contribution to the nutrient transfer process.

Nitrogen concentration in loose needles, the major component of litterfall, averaged 0.57% annually. Nitrogen concentration was highest during late winter and early spring and lowest in fall and early winter. Percentage N in bark and twigs varied little from a mean of 0.3%. Nitrogen concentration in cone

litterfall under control trees was higher than that of feed trees in May and tended to be higher throughout the year. This probably is a result of squirrel feeding activities because fewer seeds and more chewed cone and bract material were found under feed than control trees. Another possible explanation is the occurrence of differences in nutrient composition of cones between control and feed trees. Thus, perhaps trees selected by squirrels for feed trees differ nutritionally from control trees.

Abert squirrel nests serve to some extent as reservoirs or sinks for C and N. Needles, twigs, and bark of the nests had a higher percentage N than they had as components of litterfall. The duff material of nests had a greater N concentration than any of the "natural" components of litterfall. Nutrients are leached from nests by precipitation through the crown canopy and down the stem of the trees, probably at a more rapid rate than the return of nest parts with the litterfall. The latter seems very slow; only a minor fraction is apparently returned each year.

Results and conclusions in this paper are based on only one year's data. Hence, annual variations in these figures can be expected because of changes in squirrel populations, availability of other foods, and changes in feeding habits of the squirrel caused by other factors. If squirrel clipping activity were to increase to the levels Pearson (1950) reported for the 1940's, when he said it was "not unusual to find as many as 1,000 excised shoots underneath a single tree," the squirrel's impact on transfer of nutrients through litterfall might increase severalfold. Based on the present rate of transfer, even a threefold



increase in clipping activity would mean an increase of nearly 20 kg/ha/yr of N transferred. This is about twice the amount of N transferred under the control trees in this study, an amount that is close to the average for the pine forest of central Arizona (Klemmedson, unpublished data). In view of the steady state conditions that seem to prevail in the study area and in similar pine forests of Arizona, squirrel clipping activity of the magnitude described by Pearson (1950) is not likely except in local and unusual circumstances and for short durations.

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